

# A TEMNOSPONDYL AMPHIBIAN FROM THE MISSISSIPPIAN OF SCOTLAND

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**ABSTRACT.** The edopoid labyrinthodont, *Caerorhachis bairdi* (new genus and species), a specimen from Thomas Stock's collection and therefore probably from the locality of Loanhead, Midlothian, Scotland (Namurian A), has a skull structure that suggests affinities with the family Dendrerpetontidae. It has 31 presacral vertebrae, and limb proportions suggesting semiterrestrial habits, in contrast to the necessarily aquatic nature of most other known Mississippian labyrinthodonts. The vertebral structure is not of the rhachitinous type, but resembles the "protoreptilian" structure normally associated with primitive anthracosaurs. The vertebral anatomy of this animal is not consistent with the pattern expected according to Romer's theory of the evolution of the labyrinthodont centrum. Evidence from *Caerorhachis* and rhipidistian fish suggests that the specific pattern of the vertebral centra among Mississippian amphibians may be quite variable, and may not in itself be an adequate criterion for establishing the phylogenetic relationships of primitive tetrapods.

## INTRODUCTION

During the late Paleozoic, amphibians were the dominant terrestrial vertebrates. The most common of the Paleozoic amphibians were the labyrinthodonts, so called because the dentine of their teeth was infolded in the form of a labyrinth. A more important characteristic of the group is that the centra of their vertebrae were formed from more than a single ossification per segment. The pleurocentrum, comparable to the definitive centrum of amniotes, forms the posterior part of the vertebral centrum and usually supports the neural arch. The inter-

centrum, a relatively insignificant ventral element in the vertebrae of lower amniotes and absent as a discrete element in the presacral region of mammals, was an important structural element in the vertebrae of nearly all labyrinthodonts. The intercentrum forms the anterior part of the vertebra and is expressed as the haemal arch in the caudal region.

The earliest labyrinthodonts, the ichthyostegids, are known from the latest Devonian. Remains of other labyrinthodonts are common in Pennsylvanian and Permian deposits, but the group is represented by less than a dozen genera in the fossil record of the Mississippian. Consequently, our concept of the early evolution of the group is based largely on evidence provided by the study of the Pennsylvanian and Permian forms.

Among the few labyrinthodonts from the Mississippian is a nearly complete skeleton of a previously undescribed form in the collection of the Museum of Comparative Zoology at Harvard University. The description of any Mississippian amphibian is of considerable importance, but the structure of the vertebrae of this specimen makes it of particular significance in understanding the phylogeny of Paleozoic labyrinthodonts.

## ACKNOWLEDGEMENTS

We wish to thank the late Dr. Alfred S. Romer for allowing us to examine and make casts of the specimen of *Caerorhachis*. An interpretation of the structure of this animal

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would have been impossible without his extensive work on labyrinthodonts. We also wish to thank Dr. Farish Jenkins and Dr. A. W. Crompton for allowing us to continue the study of *Caerorhachis* after Dr. Romer's death. We would also like to extend our gratitude to Dr. Donald Baird, who prepared the specimen, and who was the first to recognize its importance. This work was supported by a grant from the National Research Council of Canada.

## SYSTEMATIC DESCRIPTION

Class **AMPHIBIA**

Subclass **LABYRINTHODONTIA**

Order **TEMNOSPONDYLI**

Suborder **RHACHITOMI**

Superfamily **EDOPOIDEA**

Family **DENDRERPETONTIDAE?**

*Caerorhachis*, new genus

Type species: *Caerorhachis bairdi*.

Etymology: From the Greek "*kairos*" meaning suitable, and "*rhachis*" meaning spine, in reference to the vertebral column.

*Diagnosis.* Small edopoid amphibian, skull similar to that of *Dendrerpeton* except that the postparietals are relatively narrower and longer, there is not a well developed otic notch, and the pterygoids meet anterior to the interpterygoid vacuities; palatal and medial surface of mandibles heavily denticulate; vertebrae "proto-reptilian"; pleurocentra large, horseshoe-shaped; intercentra smaller, crescentic; 31 presacral vertebrae.

*Caerorhachis bairdi*, new species

Etymology: The animal is named after Dr. Donald Baird, who first prepared the specimen and recognized its importance.

*Diagnosis.* Same as for genus.

*Holotype.* MCZ 2271, nearly complete skeleton preserved in associated blocks of coal shale. This specimen originally showed a limited exposure of bone, badly weathered, on the surface of the blocks. The external surface of the lower jaws and a large fragment of the skull roof were cast from

the original bone. All of the bone was then removed from the specimen by soaking in a dilute solution of hydrochloric acid. Silicone rubber casts were then made. These casts, replicating the original bone surface with great clarity, formed the basis for this description.

## HORIZON, LOCALITY AND HISTORY

According to Dr. Baird, the specimen was probably acquired by the Museum of Comparative Zoology in 1883 with the Thomas Stock collection of Scottish Carboniferous fish and amphibians. The specimen bore no label or written information when Dr. Baird prepared it in 1955. However, as he noted, the matrix closely resembles that of the Loanhead No. 2 ironstone, Limestone Coal Group, Namurian (E1), Upper Carboniferous. This is equivalent to the Upper Mississippian of North America.

## DESCRIPTION

*Skull.* The dorsal surface of the posterior portion of the skull table was exposed prior to preparation, together with a natural cast of part of the medial surface of the right cheek and the ventral surface of the interorbital area. This area was cast before acid preparation (Fig. 1). Following preparation, the specimen was cast again (Fig. 2). A portion of the ventral surface of the fronto-nasal region can be seen on the cast, but palatal elements obscure much of the posterior part of the skull table. During preservation, part of the left cheek was folded under the skull roof; consequently, the left postorbital and quadratojugal are visible ventrally. Another bone, lying behind the skull, is probably part of the right quadratojugal.

Although the skull roof is incomplete, and much of the surface is exposed only in internal aspect, its general structure and most of its suture patterns may be restored with reasonable confidence. The outline of the skull is provided by the nearly complete palatal. The general size and skull proportions resemble those of the primitive rhachit-

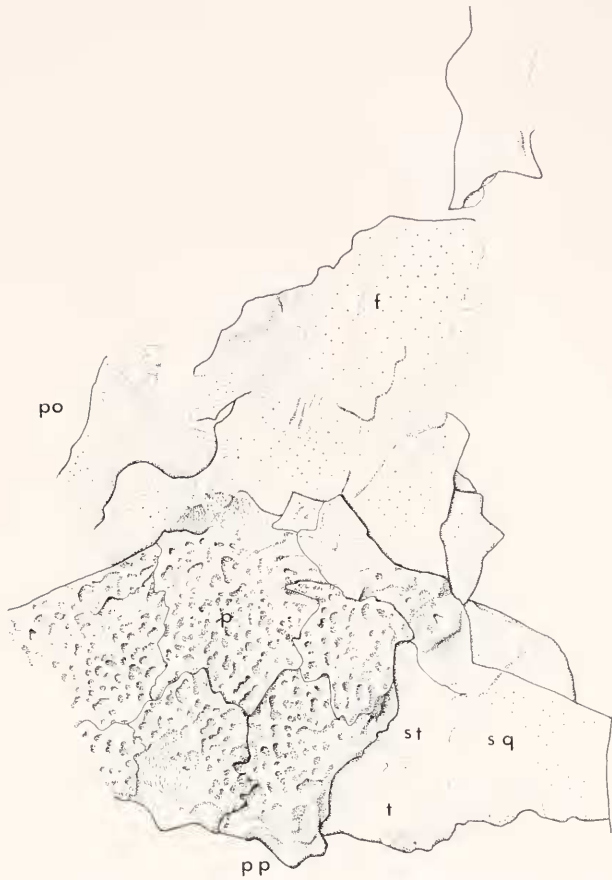


Figure 1. Skull roof of *Caerorhachis bairdi*, drawn from cast of original bone surface,  $\times 3$ . (For abbreviations for this and following illustrations, see "Explanation of Abbreviations" at end of paper.)

omous amphibian *Dendropeton* (Carroll 1967). The skull length is about 52 mm, which is roughly 1.4 times the width at the quadratojugal. The skull table is between 55 per cent and 60 per cent of the total skull width. The skull height was at least 35 per cent of its width at the quadratojugal. The quadrates are located only slightly behind the posterior margin of the skull roof as in *Dendropeton*, unlike the condition seen in *Edops* (Romer and Witter 1942), in which larger skull size has necessitated a relative increase in the size of the cheek region for the accommodation of a greater amount of adductor musculature. The posterior margin of the squamosal probably appeared concave when viewed laterally, but there is

no evidence for the existence of a well defined otic notch. The center of the orbits is slightly anterior to the middle of the length of the skull.

The external surface of the dermal bones bears the typical temnospondyl pit-and-groove sculpturing. This is most clearly shown on the postorbital and quadratojugal. None of the bones shows evidence of grooves for lateral line canals. The skull table and cheek region appear to be suturally attached, as is the case in all temnospondyls, and in contrast to the condition in primitive anthracosaurs.

Weathering has damaged the bone surface of the skull table, muting the sculpturing and rendering the determination of su-

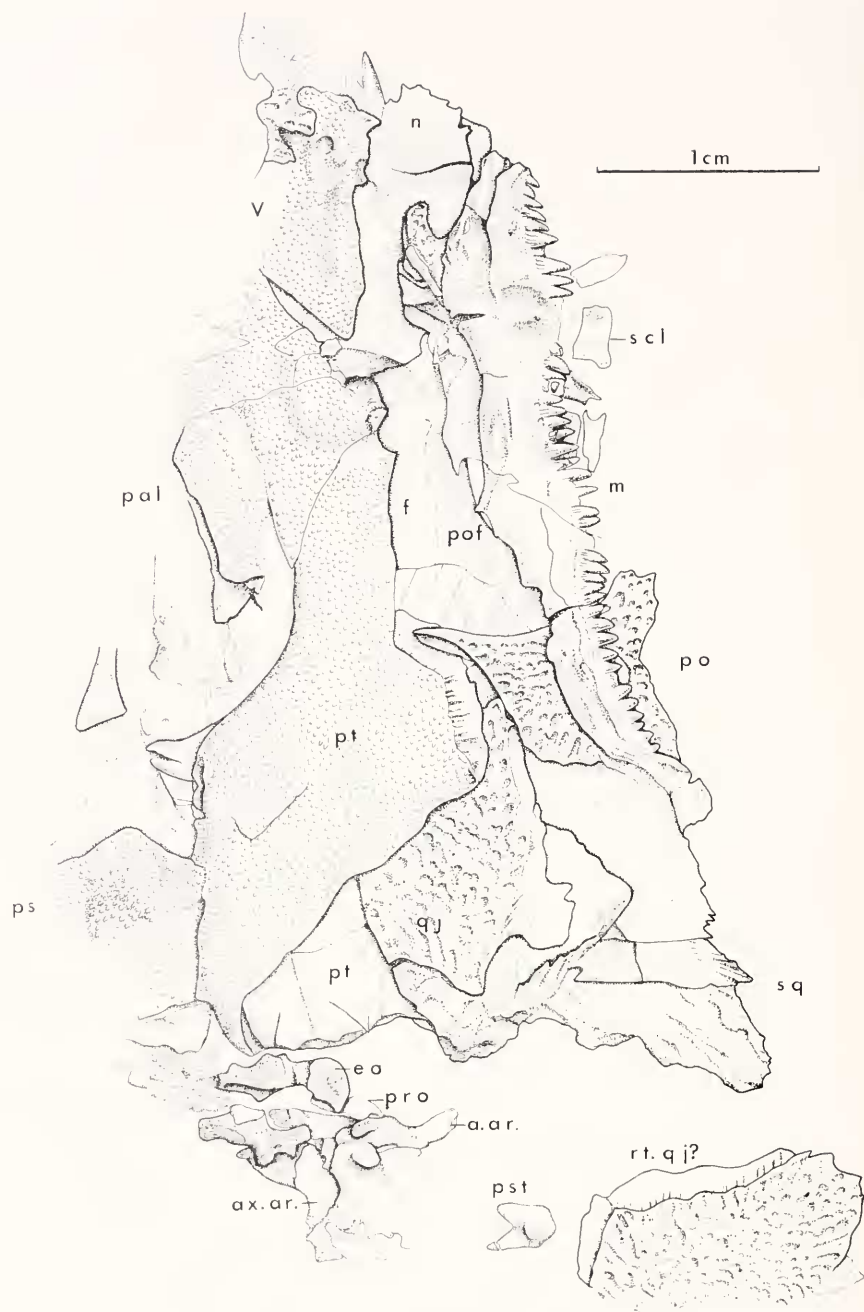


Figure 2. Disarticulated skull roof elements and ventral view of left side of palate of *Caerorhachis bairdi*,  $\times 3$ .



Figure 3. Reconstruction of the skull roof of *Caerorhachis bairdi*,  $\times 2$ .

tures difficult. The tracing of sutures was also hindered by the loss of much of the bone of the anterior part of the table. Reconstruction of this area is based partially on impressions of the internal surface of the missing bone. The pattern of the skull table is shown in Figure 3. The postparietals are characterized by posterior lappets, as in *Dendrerpeton*, that presumably descend onto the occipital surface. These bones are relatively longer and narrower than those in *Dendrerpeton*. This is presumably a primitive characteristic, judging from the condition in other Mississippian temnospondyls such as *Greererpeton* (Romer 1969) and *Pholidogaster* (Panchen 1975). The tabulars are small and are separated from the

parietals by the supratemporals. This is typical of temnospondyls and unlike the condition in anthracosaurs in which the tabulars are larger and make sutural contact with the parietals. The area of the pineal foramen is not preserved, although both the anterior and posterior limits of the parietals can be determined. The dorsal part of the right squamosal and adjacent skull roof are represented by a natural cast of the inner surface. Although the posterior borders of the right tabular and right squamosal are poorly preserved and incomplete, enough of these bones is present to indicate that the existence of a well developed otic notch is unlikely. The quadratojugal is surprisingly large, in marked contrast to that of *Dend-*

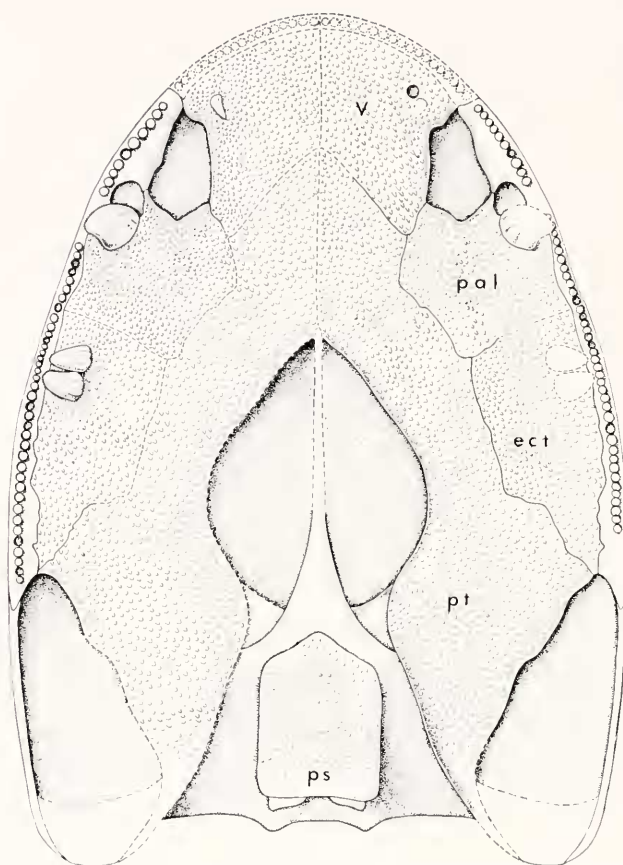


Figure 4. Reconstruction of the palate of *Caerorhachis bairdi*,  $\times 2$ .

*rerpeton*, but no larger than that noted in other primitive labyrinthodonts such as *Edops*, *Greererpeton* or *Crassigyrinus* (Panchen 1973). The jugal cannot be identified. Only a few fragments of the anterior portion of the skull roof, of little use in reconstruction, are exposed in external view (Fig. 2). Part of the frontal-nasal region is exposed ventrally, but similarly is of little help in the reconstruction of the snout region. The outline of the anterior portion of the skull can be established from the dimensions of the palate and the length of the lower jaw. Apparently the snout was broadly rounded and the external nares were widely separated.

The left maxilla is exposed medially in as-

sociation with the skull roof and palatal elements. The right maxilla remains in articulation with the margin of the palate (Fig. 5). Neither shows the tooth row in its entirety, but there appears to have been room for about 48 teeth in each maxilla. This is the same as the estimated number of maxillary teeth reported for *Dendrerpeton*. The medial surface of the left maxilla shows large depressions to accommodate the wide bases of the palatine and ectopterygoid fangs. Adjacent to the palatine fangs the margins of both maxillae appear to be devoid of teeth. Such a condition has not been described in any other labyrinthodonts. The tooth row of the left maxilla is about 10 per cent shorter than that of the

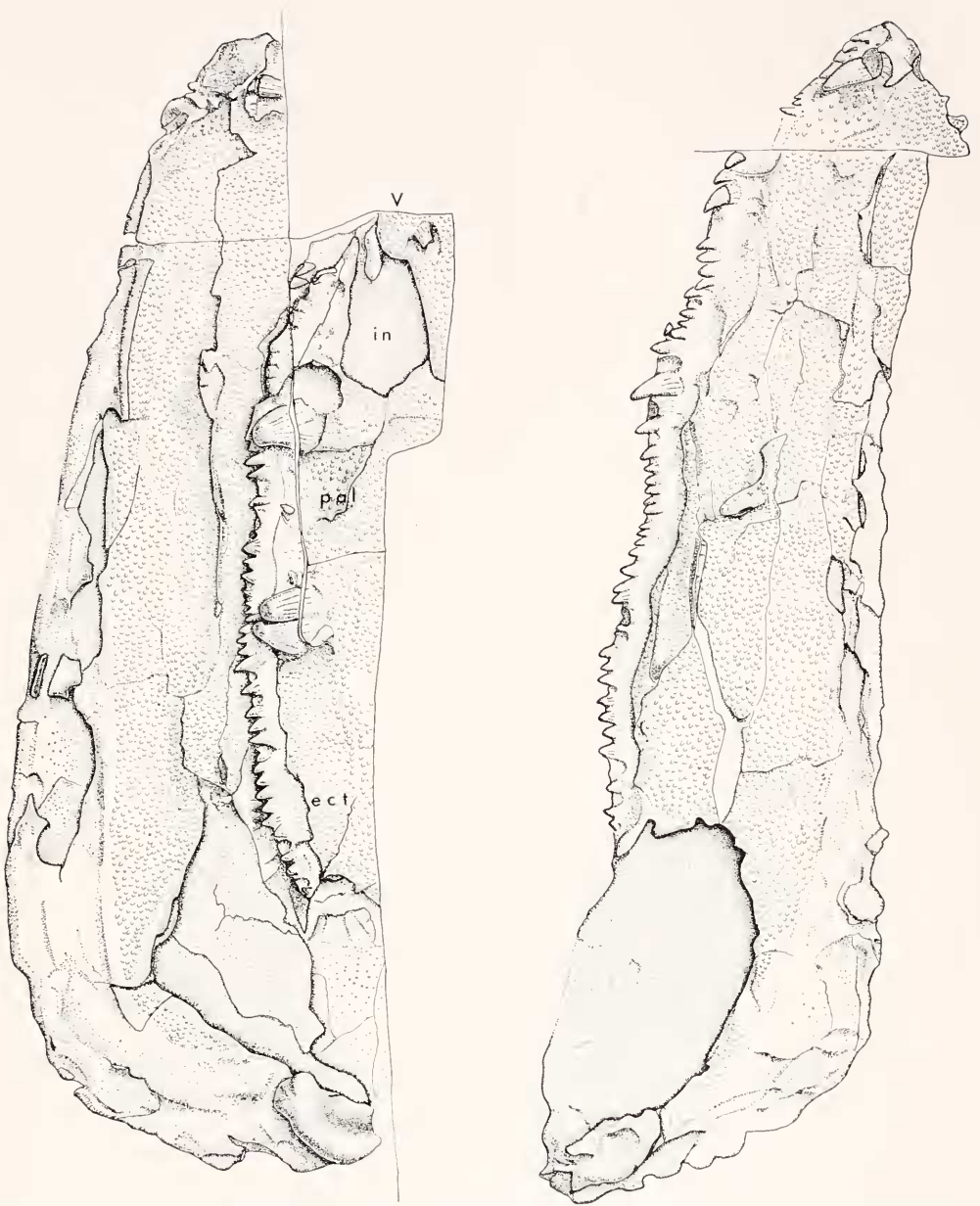


Figure 5. Right side of palate in ventral view and jaw rami in medial view of *Caerorhachis bairdi*,  $\times 3$ .

right maxilla (Fig. 4) but shows evidence of distortion during preservation. The premaxillae are not preserved. However, the width of the snout indicates that each would

have carried roughly 18 teeth, which is close to the count in *Dendrerpeton*.

Parts of the palate are preserved in two blocks. The left pterygoid, vomer, the dis-



Figure 6. External view of lower jaws of *Caerorhachis bairdi*, drawn from a cast of original bone surface,  $\times 2$ .

placed left palatine (partially covered by the pterygoid), and the parasphenoid minus the anterior part of the cultriform process, are preserved in semi-articulated fashion (Fig. 2). The other block contains the right margin of the palate from the subtemporal fossa to a point slightly anterior to the internal naris. All elements are articulated except for the vomer, which has slipped slightly medially (Fig. 5).

The entire palate, except for the cultriform process of the parasphenoid, is covered in closely packed denticles. Sutures are occasionally indistinct, but slight displacement has revealed their positions in most cases. The pterygoids met anteriorly as they

do in *Edops*. The basicranial articulation is definitely movable, as would be expected in such a primitive form. The cultriform process forms a slim rod, narrowing anteriorly. Because the remainder of the palate closely resembles that of *Dendroperpeton*, the process is restored as extending the entire length of the vacuities and inserting between the pterygoids anteriorly (Fig. 4).

The vomer, palatine and ectopterygoid each bear two fangs. Only one fang is actually present on the right palatine (the missing fang represented by an empty pit) indicating the regular replacement typical of early tetrapods. The vomerine fangs are slightly larger than the largest of the margi-

nal teeth, while those of the palatine and ectopterygoid are considerably larger than these teeth. All show typical labyrinthine infolding.

What can be seen of the medial margin of the left pterygoid indicates that the interpterygoid vacuities were relatively larger than those of *Edops*, but not as extensive as those of *Dendrerpeton*. The internal nares are large and rather square in proportion. They are quite similar in configuration and position to the internal nares of *Edops*, and quite unlike those of *Dendrerpeton*, which are relatively much larger and elongate. They are also widely separated, as is characteristic of temnospondyls. Anthracosaurs have a much narrower snout and consequently the space between these openings is much less. Fragments of the braincase can be observed in the same block containing the left side of the palate (Fig. 2). The occipital bones have become disarticulated from the rest of the skull and lie posterior to the parasphenoid. The exoccipitals are exposed in anterior view along with fragments of badly crushed bone possibly representing the remains of the otic capsule. Each exoccipital bears a rough, subcircular facet for the reception of the basioccipital. Dorsally, there is another facet that articulated with the opisthotic. Between these two articulating surfaces is a large vagus canal. A pleuracanth shark tooth lies nearby. The sphenethmoid region of the braincase has not been preserved. Sclerotic plates are present on the block containing palate and skull roof elements (Fig. 2).

Almost every feature of the skull suggests that *Caerorhachis* is an edopoid temnospondyl, similar in many ways to *Dendrerpeton*. The sculpturing is identical. The general proportions are very close, and the configuration of the bones on the skull roof is comparable. The supratemporal appears to be slightly smaller, and the intertemporal larger than in *Dendrerpeton*, but these bones are not perfectly preserved, making exact comparison of dimensions difficult. The temporal series is solidly fused to the

cheek. The absence of a well defined otic notch appears to be the main feature distinguishing this animal from *Dendrerpeton*. Two other Mississippian labyrinthodonts, *Greererpeton* and *Pholidogaster* (Panchen 1975) also lack otic notches. These two closely related forms are primitive members of the family Colosteidae, a distinct lineage of secondarily aquatic labyrinthodonts unrelated to *Caerorhachis* and other edopoids. The absence of an otic notch may be a primitive feature of labyrinthodonts (Panchen 1975), although it has been generally assumed that this notch was derived more or less directly from the spiracular cleft of rhipidistians.

*Lower Jaw.* The poorly preserved lateral bone surface of the lower jaws shows sculpturing comparable to that present on the bones of the skull roof (Fig. 6). Unlike the jaw of *Dendrerpeton*, in which only the angular and splenial bear heavy sculpturing, the entire lateral surface of the jaw of *Caerorhachis* appears to be evenly covered by coarse sculpturing. Although most of the sutures cannot be followed, the sculpture pattern indicates that the arrangement of the bones is generally like that of a typical primitive temnospondyl. The splenials have unusually large lateral exposure, which is a primitive characteristic (Romer 1947). No lateral line canals are evident.

Acid preparation has exposed the medial surfaces. Although the rami have been badly crushed, and the sutures are sometimes difficult to distinguish from cracks on the bone surface, the medial aspect of the jaw can be reconstructed with reasonable accuracy (Fig. 7). The number and shape of the bones appear to be generally similar to those of typical temnospondyl labyrinthodonts. A shagreen of denticles similar to those already noted on the palatal elements completely covers the coronoids and prearticular. Such an extensive cover of denticles on the medial surface of the mandible is exceptional in labyrinthodonts (Romer 1947). A pair of parasymphyseal tusks, comparable in size to the palatal fangs, can

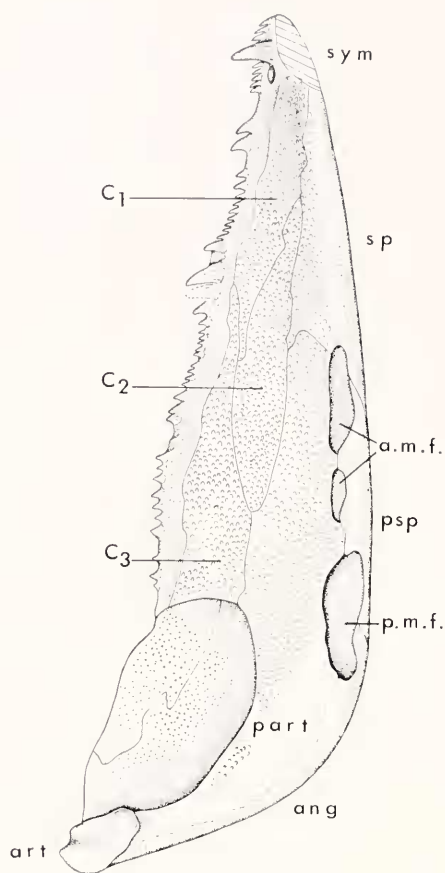


Figure 7. Reconstruction of the medial surface of the lower jaw of *Caerorhachis bairdi*,  $\times 3$ .

be seen. Although often present in temnospondyls, these structures are not common in anthracosaurs, where they have been reported only in some Mississippian embolomeres (Romer 1963) and the Pennsylvanian genus *Gephyrostegus* (Carroll 1970). The dentary has room for between 60 and 65 teeth, all of which are simple conical structures, curved slightly backwards and showing labyrinth infolding. The teeth are significantly larger at two points in the tooth row. The first peak is located at about the 18th tooth, and the second at about the 32nd.

There are three meckelian fenestrae on the medial surface of the jaw. The most

posterior is the largest, and is bordered posteroventrally by the angular, anteriorly by the postsplenial, and posterodorsally by the prearticular. Two additional fenestrae, located more anteriorly, are slightly smaller. They both appear to be bordered ventrally by splenial elements and dorsally by the prearticular.

If the short axis of the lower jaws was oriented vertically, the articulating surface of the articular bone would face medio-dorsally, rather than directly dorsally. This indicates that, when in articulation, the jaw of *Caerorhachis* must have been tilted medially to a greater degree than in most labyrinthodonts. Romer and Witter noted a similar situation in *Edops*. Consequently, the medial surface faced obliquely dorsally toward the palate, and when the jaws were clamped shut they would have forced the prey up onto the palate. Presumably the thick and complete covering of denticles present on the palate and inner surface of the mandibles assisted the palatal fangs and marginal teeth in holding the prey.

*Axial skeleton.* The atlas-axis complex is preserved immediately behind the skull. The two halves of the atlas arch (Fig. 2) appear to have been coössified. The neural spine of the right half of the arch is a thin process, directed dorsoposteriorly, as described for *Eryops* (Moulton 1974). The anterior zygapophysis, for articulation with the proatlas, is located on a tubercle on the lower, anterodorsally facing surface of the spine. The posterior zygapophysis is not visible. The pedicle of the left half of the atlas arch is exposed in lateral view. The left proatlas lies close to the anterior zygapophysis. The pedicle of the left axis arch can be seen in medial view, exposing an extensive surface of articulation with the centrum. Unfortunately, no central elements of the atlas-axis complex have been preserved.

The remainder of the column is exposed in lateral aspect in semi-articulated fashion in the largest block (Fig. 8a, 9). It is not certain whether the most anterior of these

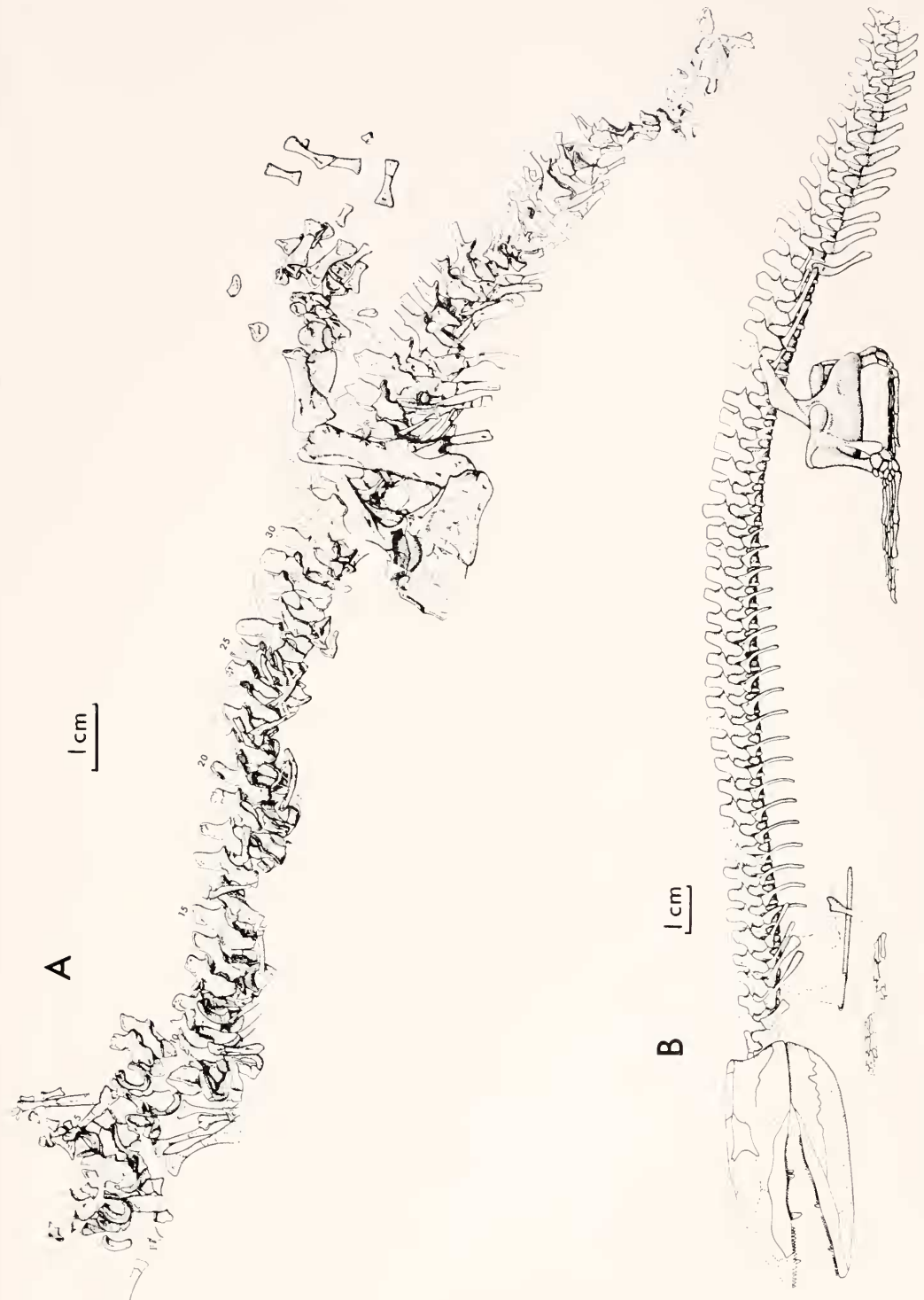


Figure 8. A, postcranial skeleton of *Caerorhachis bairdi*. This drawing is enlarged and presented in sections in Figure 9. B, stylized reconstruction of *Caerorhachis bairdi*. Scale indicated in both drawings.

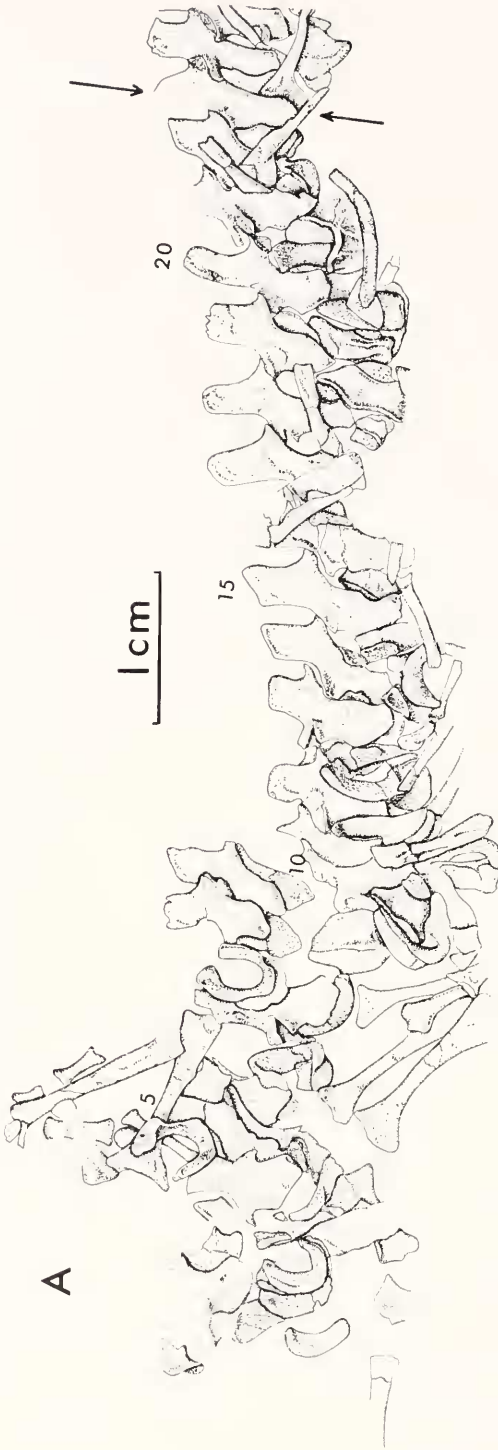
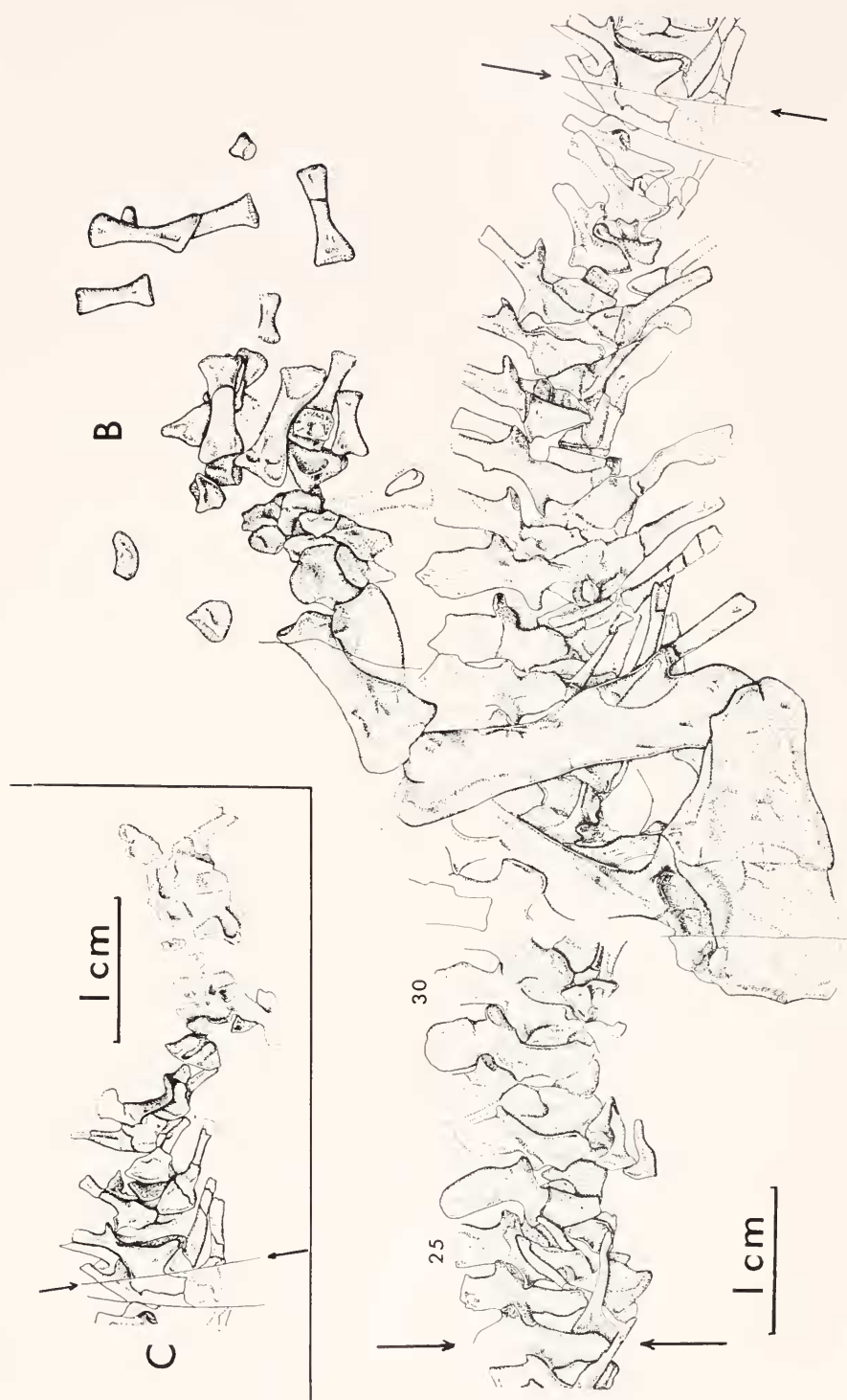


Figure 9. Postcranial skeleton of *Caerorhachis bairdi*, reproduced in sections. A, anterior trunk; B, sacral region; C, tip of tail. Arrows indicate comparable position of successive sections. Numbers indicate approximate position of presacral vertebrae.



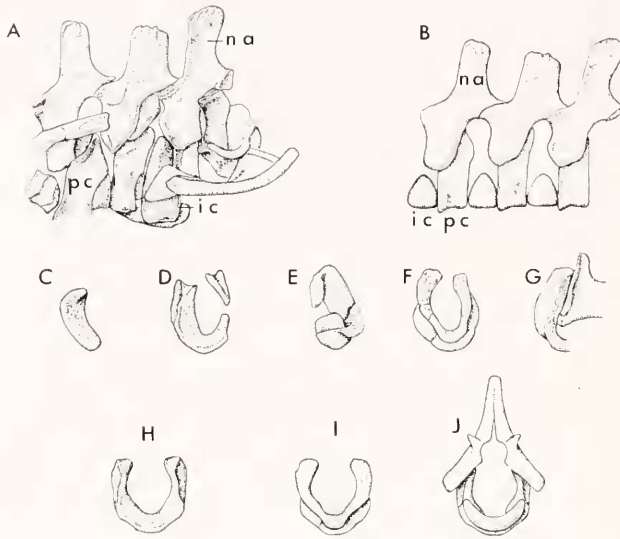


Figure 10. Elements of the vertebral column of *Caerorhachis bairdi*. A, 18th, 19th and 20th vertebrae, lateral view; B, restoration of 18th, 19th and 20th vertebrae, lateral view; C, ic 3; D, pc 3; E, pc 6; F, pc 7; G, pc 10; H, restoration of pc, anterior view; I, restoration of pc, posterior view; J, restoration of vertebra, anterior view. All  $\times 2$ .

vertebrae represents the third cervical. The configuration of the associated ribs reveals that the first several vertebrae in the block are cervicals, and unless the animal has an unusually long neck, few if any vertebrae are missing in the series.

The pelvic girdle is disarticulated from the column and slightly displaced, so there is some question as to the position of the sacral vertebra. A structure which appears to be a sacral rib is present, but it is not clear whether it is associated with vertebra 31, 32 or 33. Haemal spines can only be identified definitely as far anteriorly as the 38th vertebra. Caudal ribs, however, are present as far anteriorly as the 33rd vertebra. This evidence points to the 32nd vertebra being the sacral, which makes the presacral column of *Caerorhachis* considerably longer than that of *Ichthyostega*, the oldest known amphibian. *Ichthyostega* has a presacral count of 23 or 24 according to Jarvik's reconstruction (Jarvik 1955). However, it may be significant that the presacral column of *Eusthenopteron*, a member of the group of crossopteryg-

ians giving rise to amphibians, is 32 (Andrews and Westoll 1970a). This count is also recorded in the oldest known reptile having a well articulated column (Carroll 1969).

The central elements of the vertebrae have been dissociated from each other and the arches, making reconstruction somewhat difficult, but providing additional information concerning the structure of the individual units. Study of the central elements visible along the column reveals two very distinct structural units (Fig. 10). One type is a simple, thin crescent when viewed anteriorly. These elements are similar to the intercentra of typical labyrinthodonts. The dorsal extension of the "horn" of the crescent would probably reach no further than midway in the height of the other central element. The other element, surely a pleurocentrum, is horseshoe-shaped when viewed end-on, and midventrally about the same length as the intercentrum. Its dorsal extension is greater, however, and on each antero-dorsal surface is an articulating facet for the pedicle of the neural arch. A few of these elements remain in articulation with

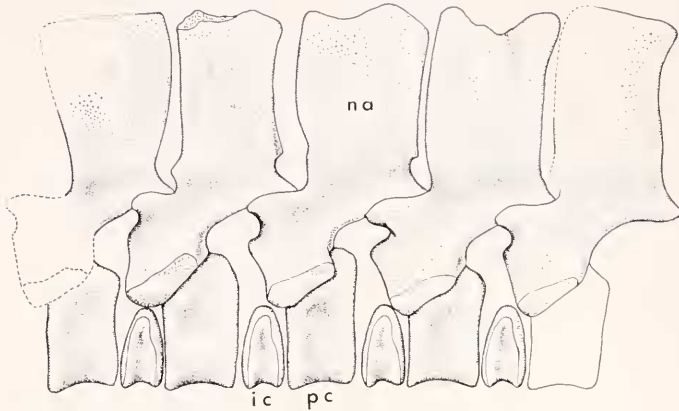


Figure 11. Dorsal vertebrae of *Proterogyrinus scheelei*,  $\times 1$ .

their respective arches. Neural arches seven and eight each show an extensive unfinished area covering most of the medial surface of the pedicle. Although the arch and pleurocentrum were not solidly fused together, such a broad contact between the two elements must have allowed them to function as a single structural unit when in articulation. The anteroventral surfaces of the pleurocentra appear to be concave, matching well with the convex surfaces of the intercentra. This would produce a functional ball-and-socket joint between the intercentrum and the pleurocentrum behind it. Though the pleurocentrum supports the arch, it is quite thin-walled, only sheathing the notochord and probably not constricting it appreciably. Primarily notochordal vertebral columns are not uncommon among primitive labyrinthodonts, especially in small forms. In *Gephyrostegus* the pleurocentrum is also horse-shoe-shaped and supports the neural arch, to which it is only weakly attached. The intercentra fit between the pleurocentra, surrounding the notochord ventrally.

*Dendroperpeton*, although unlike *Caerorhachis* in that it has typically rhachitomous vertebrae, is similar in having very thin-walled central elements which barely constrict the notochord. The vertebrae of the Upper Mississippian anthracosaur *Proterogyrinus* (Romer 1970) (Fig. 11) are quite

similar to those of *Caerorhachis*, the main difference being the heavier construction of the pleurocentrum.

The neural spines are rectangular in lateral view, and many bear conspicuous grooves on their lateral surfaces, presumably indicating the points of ligament attachment. There is little regional variation in the morphology of the neural arches except with respect to the height of the spines. The spines of the arches immediately posterior to the sacrum are the tallest. The anterior cervicals are the shortest. The height of the spine of the seventh presacral, the most anterior vertebra in which the spine is completely preserved, is about 65 per cent of the height of the spines of the anterior caudals. The spine of the 28th presacral is intermediate in height, about 80 per cent that of the anterior caudals.

Although the vertebrae have been crushed laterally, it is apparent that the neural arches were not swollen, and the zygapophyses were close to the midline as in most other primitive amphibians and most reptiles. It is impossible to measure the angles of the zygapophyses accurately because of crushing, but the posterior zygapophyses appear to face ventrolaterally at an angle of roughly 45 degrees from the sagittal plane. Well defined articulating surfaces for the



Figure 12. Dorsal view of clavicle, interclavicle and forelimb elements of *Caerorhachis bairdi* found in association with the elements in Fig. 5,  $\times 3$ .

attachment of ribs are not visible on the arches or on the central elements.

The cervical ribs are long and flattened. Both proximal and distal ends are expanded. They are double-headed, although a web of bone between the two heads tends to obscure this. Such large cervical ribs were probably necessary for the attachment of heavy neck musculature supporting the large head. The dorsal ribs are poorly preserved, but appear to have been short and rather fragile. They also appear to be two-headed, but the heads are approximately circular in cross section, unlike those of the cervical ribs. Only the first few caudal vertebrae have ribs associated with them. These ribs are even smaller and more fragile than the thoracic ribs. It is not possible to determine the nature of their articulating

surfaces. They are gently curved and appear to have been directed posteriorly in life. Both the neural and haemal spines of the caudal vertebrae are quite long and the tail is consequently quite tall and appears laterally compressed. It was probably an effective swimming organ.

**Appendicular skeleton.** The anterior end of the interclavicle is preserved in dorsal view (Fig. 12), showing a fimbriated margin. None of the posterior end of the bone is preserved. The medial portion of the ventral plate of the right clavicle is exposed in dorsal view, in articulation with the interclavicle. It is poorly preserved, however, and no details of its structure can be determined. The scapulocoracoids are not present.

Next to the interclavicle can be seen the

proximal portion of the ulna, showing a well ossified olecranon. Adjacent is another bone, presumably the radius, and what could be a small fragment of the humerus. The size of these elements indicates that the forelimbs were small. The ulna is about 20 per cent the length of the skull. It is impossible to estimate the length of the humerus.

Two metacarpals and three toe bones are preserved with the other remains of the forelimb. No carpals are present. Two more metacarpals, two phalangeal elements and one terminal phalanx are preserved in association with the cervical vertebrae, and are presumably from the other manus. The hand has been reconstructed with four toes, but without any specific evidence.

The pelvic girdle (Fig. 9) is typical of primitive temnospondyls and is quite similar to that of the edopoid *Dendrerpeton*. Although the left half of the pelvic girdle is slightly crushed and the pieces somewhat displaced, the morphology of the structure is quite clear. The ilium, ischium and pubis are all well ossified, and the sutures are indistinct. A prominent buttress is evident above the acetabulum. Below the acetabulum the plate for muscle attachment, formed by the union of the pubis and the ischium, shows a definite concave surface. The obturator foramen is not visible.

The dorsal portion of the ilium is obscured by vertebral elements and the shaft of the femur. However, it is certain that it is a simple structure which passed postero-dorsally in life to about the level of the zygapophyses of the vertebral column. There is definitely no anterior extension of the ilium, such as is present in most primitive anthracosaurs.

The left femur is preserved in dorsal view. It is basically a cylindrical structure with expanded ends, as is the case with most tetrapods. Most of the adductor crest is hidden from view, but a prominent internal trochanter projects from the anterior edge of the femur near its proximal end. The total length of the femur is about 50

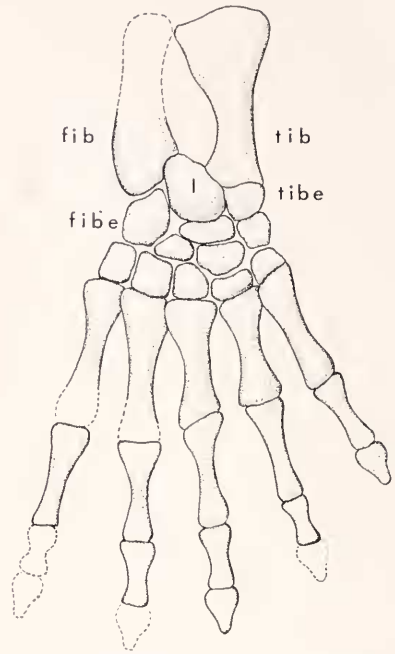


Figure 13. Reconstruction of the pes of *Caerorhachis bairdi*,  $\times 2$ .

per cent of the length of the skull. A well preserved tibia lies in articulation with the distal end of the femur. It is a stout bone, with a proximal end as wide as the distal end of the femur. The tibia is about 40 per cent of the length of the femur. The proximal end of the fibula is covered by the tibia. The distal ends of the fibula and tibia are of approximately equal width.

The tarsus appears to be essentially complete. Many of the bones are incompletely exposed, however, and their exact shape cannot be determined. The reconstruction of the foot (Fig. 13) shows a tibiale, intermedium, fibulare, four centralia of roughly equal size, and five distal tarsals, also of roughly equal size. The rest of the pes is disarticulated and scattered slightly, but there is no evidence to suggest that many of the bones are missing. Five metatarsals, eight proximal phalangeal bones, and two unguals can be clearly seen. Although it is conceivable that one more proximal phalan-



Figure 14. Ventral scales of *Caerorhachis bairdi* found in association with trunk vertebrae 20 through 30,  $\times 2$ .

geal bone is also missing (which would give *Caerorhachis* a typical temnospondyl count of 2, 3, 3, 3, 3), it is highly unlikely that more elements have been lost. The phalangeal formula of *Caerorhachis* is here restored as 2, 3, 3, 3, 3; it certainly would not have been as high as that common in anthracosaurs (2, 3, 4, 5, 5).

A portion of the ventral armor is present in the block containing the vertebral column (Fig. 14). The individual scales can be seen as being quite long and stout. They collectively make a very heavy shield covering the ventral portion of the abdomen and probably extending from the interclavicle to the pelvic girdle.

## HABITS

The absence of lateral line canal grooves on the skull roof and lower jaws and the presence of relatively large limb bones suggests that *Caerorhachis* was not tied to the water as were other known temnospondyl amphibians from the Mississippian such as *Greererpeton*, *Pholidogaster* and possible loxommatids. The presacral vertebral count is substantially lower than in the known members of these groups, although it is somewhat higher than that indicated for *Ichthyostega*.

*Caerorhachis* is here termed "terrestrial" only in a relative sense. This genus may yet have spent much of its life in the water. It shows no specializations toward locomotion in this medium, such as are evident in all other known Mississippian temnospondyls and embolomeres, although the laterally compressed tail could have served as a swimming organ. One might visualize this animal spending much of its life in the damp mud on the margins of ponds or streams, feeding on stranded fish, or occasionally venturing into the water to catch aquatic larvae of other amphibians.

## DISCUSSION

The general morphology of the skull and appendicular skeleton identify *Caerorhachis* as a primitive temnospondyl amphibian. As in typical temnospondyls, the tabular is a small bone and makes no contact with the parietal. The cheek is solidly fused to the skull table. The sculpturing on the dermal bones is of the typical temnospondyl pit-and-groove type. The internal nares are widely separated. The interpterygoid vacuities are quite wide, while those of anthracosaurs are only narrow slits. The ilium does not have the distinct anterior process characteristic of many anthracosaurs.

Primitive characteristics such as the presence of an intertemporal bone and a movable basicranial articulation, as well as the absence of lateral line canal grooves, indicate that this animal may be placed within the Superfamily Edopoidea. Furthermore, the general anatomy of the skull roof, palate and pelvic girdle shows that it is closely related to previously described members of the Family Dendrerpetontidae. The absence of a well defined otic notch makes it awkward to include *Caerorhachis* within this family as currently understood, however. The nature of the vertebrae presents a much more serious problem to the classification of *Caerorhachis*. The vertebrae are well preserved and readily reconstructed. Their structure, however, is entirely different from that seen in *Dendrerpeton* and other edopoids, and is of a type totally unexpected in primitive temnospondyl amphibians.

The structure of the vertebrae has been the basis for the major subdivisions of Paleozoic amphibians according to all recent authors. The first workable classification of labyrinthodonts was developed by Watson (1919, 1926). He considered that the vertebrae of all known labyrinthodonts conformed to one of three structural stages and he used these differences as a basis for dividing the Labyrinthodontia into the Orders Embolomeri, Rhachitomi and Stereospondyli. In the Embolomeri both the intercentrum and the pleurocentrum are complete rings, forming a "double" centrum. The Rhachitomi have vertebrae composed of large crescentic intercentra and pleurocentra represented by small paired blocks situated dorsally, posterior to the intercentrum. In the Stereospondyli, the pleurocentra have completely disappeared, and the centra are composed of only cylindrical intercentra. At the time Watson wrote, most of the known Permian labyrinthodonts had the rhachititous type of vertebrae and most of the Triassic forms stereospondylous. Little was known of the vertebral structure of Carboniferous labyrinthodonts, but the few

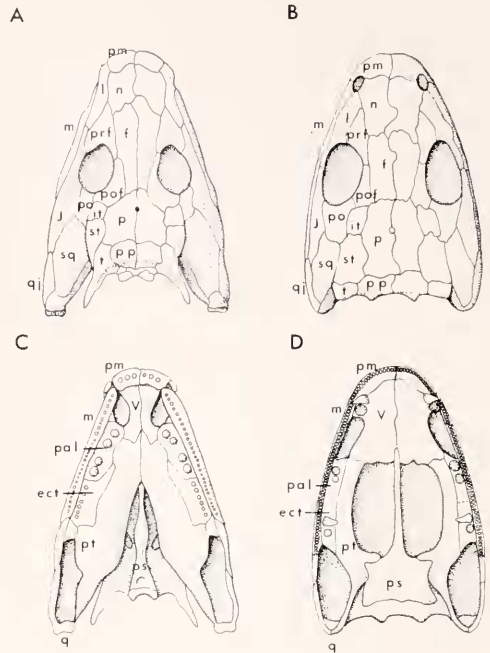


Figure 15. A comparison of the anthracosaur and temnospondyl skull. A and C, skull of *Paleoherperton*, an anthracosaur, in dorsal and ventral views; B and D, skull of *Dendrerpeton*, a temnospondyl, in dorsal and ventral views. Not to scale. A and C from Panchen (1964). B and D from Carroll (1967).

specimens in which the columns were preserved showed an embolomeric pattern. On this basis Watson concluded that the embolomeres were the primitive labyrinthodont stock. He suggested they gave rise, some time late in the Carboniferous, to the rhachitomes on the one hand and reptiles on the other.

Romer (1947, 1966), to whom more information was available, revised Watson's classification. Romer used differences in vertebral structure as a basis for his new classification but also attached considerable importance to the association of certain features of the cranial anatomy with specific vertebral patterns. The relationship of the parietal and tabular is of particular importance. The tabular is large in embolomeres and other anthracosaurs and has sutural

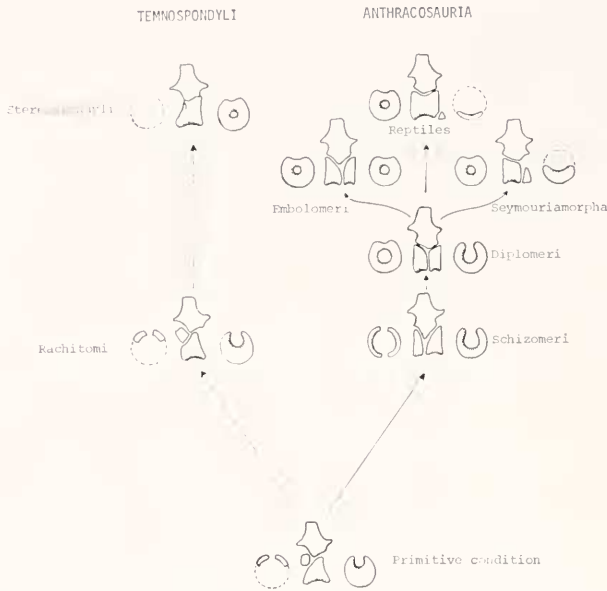


Figure 16. Romer's scheme for the evolution of the labyrinthodont centrum. Adapted from Romer (1966).

contact with the parietal. In temnospondyls, the tabular is small and separated from the parietal by the supratemporal, except in the Middle Permian genera *Intasuchus* and *Syndyosuchus* (Konjukova 1956).

In Romer's scheme (Fig. 16), the rhachitomous vertebral pattern is considered primitive for labyrinthodonts. The rhachitomes are suggested as having given rise to the stereospondylous pattern by elimination of the paired pleurocentra and enlargement of the intercentrum, and to the embolomerous pattern by fusion of the paired pleurocentra ventrally and dorsally to form a ring, together with dorsal elaboration of the intercentrum. Romer united rhachitomes and stereospondyls within the Order Temnospondyli. The embolomeres plus the specialized seymouriamorphs made up the Order Anthracosauria.

Evidence which has come to light since Romer's classification was first proposed has tended to support it. *Ichthyostega*, the oldest known amphibian (Upper Devonian), was identified by Romer as being a temnospondyl, although it was known only

from skull remains when he first proposed his classification in 1947. This was apparently confirmed by Jarvik's (1952) description of the postcranial skeleton, although the vertebrae were closer in appearance to those of some rhipidistian crossopterygians than to those of typical rhachitomes. The loxommatids, common in the Carboniferous, were also included by Romer in the Rhachitomi because of their skull roof pattern, although the structure of the vertebral column was unknown in 1947. Baird (1957) later described rhachitomous vertebrae associated with the Carboniferous loxommatid *Megalocephalus*.

Romer (1964) found it necessary to hypothesize an intermediate stage, which he termed "schizomerous," to illustrate the transition from the rhachitomous vertebral pattern to that characteristic of anthracosaurs. In this condition, the pleurocentrum was still a paired element, as in rhachitomes, but the two halves extended more ventrally, almost meeting at the ventral midline. Fusion of these elements ventrally in subsequent forms would have produced a proper

anthracosaurian centrum. Further elaboration of the pleurocentra and reduction of the intercentrum could give rise to the reptilian condition. Romer suggested that *Pholidogaster*, a Lower Carboniferous labyrinthodont, displayed such an intermediate vertebral structure and could be considered as an ancestor of anthracosaurs.

At the time of the publication of Romer's 1964 paper, it seemed that all Paleozoic labyrinthodonts could be fitted into a single, simple phylogenetic progression, with the primitive rhachitomous pattern ancestral to all the vertebral diversity seen in the group. Subsequently, information has accumulated that necessitates re-examination of this scheme.

Recent preparation of the skull of *Pholidogaster* reveals that this animal is not at all closely related to embolomeres but, rather, is a primitive colosteid temnospondyl (Panfili 1975). *Proterogyrinus*, and the probably synonymous *Mauchchunkia* from the Upper Mississippian, were described respectively by Romer (1970) and Hotton (1970). Although this material pertains to an anthracosaur of great age and very possibly one ancestral to later members of that group, its vertebrae do not give any indication of the "schizomerous" structure that Romer hypothesized as being intermediate between the rhachitomous and anthracosaurian vertebral patterns. Instead, the vertebrae are almost reptilian in nature, each with a well developed, horseshoe-shaped pleurocentrum and smaller crescentic intercentrum (Fig. 11). This material makes it difficult to accept Romer's hypothesis that the anthracosaurian vertebral configuration was evolved from the rhachitomous or proto-rhachitomous pattern.

Questions have also been raised as to the suggested rhachitomous or proto-rhachitomous pattern of the vertebrae of *Ichthyostega* and *Eusthenopteron*. Thomson and Vaughn (1968) in their description of *Lohsania*, a rhipidistian with vertebrae somewhat similar to those of *Eusthenopteron*, suggested that the major vertebral elements

in this animal represent both the pleurocentrum and the intercentrum in tetrapods. According to Thomson and Vaughn, the vertebral element identified by Romer as a pleurocentrum in rhipidistians such as *Eusthenopteron* and in *Ichthyostega* is actually an accessory arch element. However, exhaustive analysis of several rhipidistian genera by Andrews and Westoll (1970a, 1970b) confirms the identity of the pleurocentrum in these fishes.

Discovery of a more or less anthracosaurian vertebral structure in the oldest terrestrial temnospondyl confuses the picture even more. There are a number of ways in which the vertebral pattern of *Caerorhachis* may be viewed. As the only known "terrestrial" temnospondyl amphibian from the Mississippian, it may simply be exceptional in its vertebral structure—a peculiar departure from a common rhachitomous pattern. Other closely related forms might resemble *Dendrerpeton* in vertebral as well as cranial structure. This interpretation conforms with Romer's suggestion that the rhachitomous pattern was basic to all temnospondyls.

One might, in contrast, emphasize the importance of the similarity of the vertebral structure of *Caerorhachis* to that of early anthracosaurs such as *Proterogyrinus* and *Gephyrostegus*. It is certainly of some significance that the earliest members of each of these respective lineages have nearly identical vertebral patterns. We were at one stage tempted to suggest that the common possession of a proto-reptilian vertebral pattern in these forms indicated that this was the primitive structure for labyrinthodonts. One can even interpret that structure in *Ichthyostega* as comparable. If the paired dorsal elements are not pleurocentra, the dominant crescentic element in that genus is functionally somewhat comparable to the horseshoe-shaped pleurocentra of *Proterogyrinus* and *Caerorhachis*. One immediate problem of this interpretation of *Ichthyostega* is that the intercentrum, an important element of all laby-

rithodonts, is thus unaccounted for. Our knowledge of higher temnospondyls makes it difficult to accept that the rhachitomous pattern was achieved by a reduction of the pleurocentrum from the pattern seen in *Caerorhachis*. A mechanical explanation, such as that proposed by Parrington (1967), might account for such a modification in large terrestrial derivatives, but does not explain the common presence of a rhachitomous pattern in aquatic loxommatids and colosteids as well as in edopoids (other than *Caerorhachis*) and eryopoids.

It remains much easier to retain the assumption that the rhachitomous pattern is fundamental to Pennsylvanian and Permian temnospondyl amphibians. This indicates that the pattern in *Caerorhachis* is distinctive, but this may be more a matter of superficial appearance than of functional significance. It must be emphasized that the ossified and fossilized elements of the vertebral column in *Caerorhachis*, *Gephyrostegus* and *Dendrerpeton*, and to a variable extent other small or primitive labyrinthodonts, do not occupy more than a small portion of the total structure. The column remains functionally notochordal, with an unknown amount of more resistant cartilage between and medial to the ossified elements. This situation is, in fact, not greatly different from that encountered in rhipidistians (Andrews and Westoll 1970a, b). In that group, the column is fundamentally notochordal, but with a considerable variety of vertebral ossifications. There is no obvious association of particular patterns with the various taxonomic groups. Apparently there are a number of different ways of solving similar functional requirements. This situation may pertain also among primitive and small amphibians. It may be expected that there would be a considerable variety of vertebral structures among Mississippian labyrinthodonts, particularly among the smaller forms. Different configurations may not, however, have much functional or phylogenetic significance, as long as the column as a whole is primarily notochordal. With

increase in size and degree of vertebral ossification, the pattern increases in functional and phylogenetic significance. Within the Pennsylvanian the structure has become stabilized so that few, if any, exceptions are known to the pattern of intercentral dominance among temnospondyls and pleurocentral dominance in anthracosaurs. Within the Mississippian, however, it would seem possible that members of both of these orders, as established by the structure of the skull, could have a variety of patterns of the superficial vertebral ossification. The presence of one pattern would not necessarily preclude close relationship to forms with quite a different structure. At this stage, the amount and specific distribution of cartilage and bone at the surface of the notochord is clearly of less phylogenetic significance than it is in the Pennsylvanian and Permian.

The possibility of extensive plasticity within the vertebral patterns of Mississippian tetrapods indicates that it may be difficult, if not impossible, to establish any particular pattern as primitive, or to trace in any simple, straightforward way, the derivation of any of the specialized patterns from one another. The vertebral structure seen in *Caerorhachis* emphasizes these problems; further evidence may be expected from additional discoveries of labyrinthodonts from the Lower Carboniferous.

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## EXPLANATION OF ABBREVIATIONS

|                                  |                               |                             |
|----------------------------------|-------------------------------|-----------------------------|
| a. ar.—atlas arch                | in—internal naris             | psp—postsplenial            |
| a.m.f.—anterior meckelian fossae | it—intertemporal              | pst—pleuracanth shark tooth |
| ang—angular                      | j—jugal                       | pt—pterygoid                |
| art—articular                    | l—lacrimal                    | q—quadrate                  |
| ax. ar.—axis arch                | m—maxilla                     | qj—quadratojugal            |
| c <sub>1</sub> —1st coronoid     | n—nasal                       | rad—radius                  |
| c <sub>2</sub> —2nd coronoid     | na—neural arch                | rt. qj.—right quadratojugal |
| c <sub>3</sub> —3rd coronoid     | p—parietal                    | sa—surangular               |
| cl—clavicle                      | pal—palatine                  | scl—sclerotic plate         |
| d—dentary                        | part—prearticular             | sp—splenial                 |
| ect—ectopterygoid                | pc—pleurocentrum              | sq—squamosal                |
| eo—exoccipital                   | pm—premaxilla                 | st—supratemporal            |
| f—frontal                        | pmf—posterior meckelian fossa | sym—symphysis               |
| fib—fibula                       | po—postorbital                | t—tabular                   |
| fibe—fibulare                    | pof—postfrontal               | tib—tibia                   |
| hum—humerus                      | pp—postparietal               | tibe—tibiale                |
| l—intermedium                    | prf—prefrontal                | ul—ulna                     |
| ic—intercentrum                  | pro—proatlas                  | v—vomer                     |
| icl—interclavicle                | ps—parasphenoid               |                             |